



Rands, SA., Pettifor, RA., Rowcliffe, JM., & Cowlshaw, G. (2004). State-dependent foraging rules for social animals in selfish herds. *Proceedings of the Royal Society B: Biological Sciences*, 271(1557), 2613 - 2620. <https://doi.org/10.1098/rspb.2004.2906>

Peer reviewed version

Link to published version (if available):
[10.1098/rspb.2004.2906](https://doi.org/10.1098/rspb.2004.2906)

[Link to publication record in Explore Bristol Research](#)
PDF-document

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

State-dependent foraging rules for social animals in selfish herds

Sean A. Rands^{1,2*}, Richard A. Pettifor¹, J. Marcus Rowcliffe¹ and Guy Cowlshaw¹

¹*Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK*

²*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*

Many animals gain benefits from living in groups, such as a dilution in predation risk when they are closely aggregated (referred to as the 'selfish herd'). Game theory has been used to predict many properties of groups (such as the expected group size), but little is known about the proximate mechanisms by which animals achieve these predicted properties. We explore a possible proximate mechanism using a spatially explicit, individual-based model, where individuals can choose to rest or forage on the basis of a rule-of-thumb that is dependent upon both their energetic reserves and the presence and actions of neighbours. The resulting behaviour and energetic reserves of individuals, and the resulting group sizes, are shown to be affected both by the ability of the forager to detect conspecifics and areas of the environment suitable for foraging, and by the distribution of energy in the environment. The model also demonstrates that if animals are able to choose (based upon their energetic reserves) between selecting the best foraging sites available and moving towards their neighbours for safety, then this also has significant effects upon individuals and group sizes. The implications of the proposed rule-of-thumb are discussed.

Keywords: social foraging; optimization; perceptual range; group size

1. INTRODUCTION

When animals form groups, it is often assumed that each individual faces various costs and benefits of group membership (Pulliam & Caraco 1984; Giraldeau & Caraco 2000; Krause & Ruxton 2002). For example, within a foraging group, benefits could come through an increased likelihood of finding food or detecting predators, while costs could come through increased competition for resources, or increased visibility to predators. Much theoretical work has been conducted examining how the trade-off between these costs and benefits can determine the stable size of a group (Clark & Mangel 1984; Ekman & Rosander 1987; Sibly 1983; Higashi & Yamamura 1993; Giraldeau & Caraco 2000), and how these predictions match with empirical observations (Krause & Ruxton 2002). However, although these studies have considered which group sizes should be stable from a functional perspective, little work has been conducted examining the proximate mechanisms resulting in the formation of these groups: recent models (e.g. Flierl *et al.* 1999; Juanico *et al.* 2003) have considered the actions of individuals following extremely simple rules-of-thumb. However, as noted by Krause & Ruxton (2002), little consideration has been given to making these rules realistic. State-dependent models of behaviour (Clark & Mangel 2000; Houston & McNamara 1999) offer us a means of predicting realistic rules, by considering which behaviours at a particular moment in time an animal with a given state set (such as its energy reserves, or the environment it currently occupies) should conduct in order to maximize some measure of its fitness. Therefore, unlike previous spatially explicit models

considering group formation behaviour, the model presented in this paper bases its rules upon the results of state-dependent models (Rands *et al.* 2003).

The moment-to-moment decisions about movement made by an animal will depend upon a number of factors. For example, if it is foraging, it may move in order to visit patches that yield the highest nutrient content. However, if the environment is dangerous, it may choose its movements in order to minimize its risk of predation, which could be done by altering its behaviour (Houston & McNamara 1999) or by choosing its environment according to its relative level of risk (Cowlshaw 1997). Within groups, other predation-reducing behaviours are available: in joining a group, the risk to an individual is diluted, and its spatial position within the group may be important (Krause 1994; Stankowich 2003). Hamilton (1971) explored this 'selfish herd' concept, and demonstrated that in order to reduce predation risk (where it is assumed that a randomly appearing predator will attack the nearest prey item) an individual should minimize the amount of unoccupied space around itself from which a predator would selectively target it as a victim. Furthermore, choosing when to forage in relation to what neighbours are doing may bring benefits through increased predator detection or energetic gain (Rands *et al.* 2003), where theory suggests that the activities of the foragers should become highly synchronized if there is a fitness-increasing advantage to foraging or resting together. However, in conducting 'selfish herding' behaviour, the forager faces a trade-off; although its predation risk is reduced, it is likely that its energy intake will be reduced as well (Krause & Ruxton 2002).

* Author for correspondence (s.rands@zoo.cam.ac.uk).

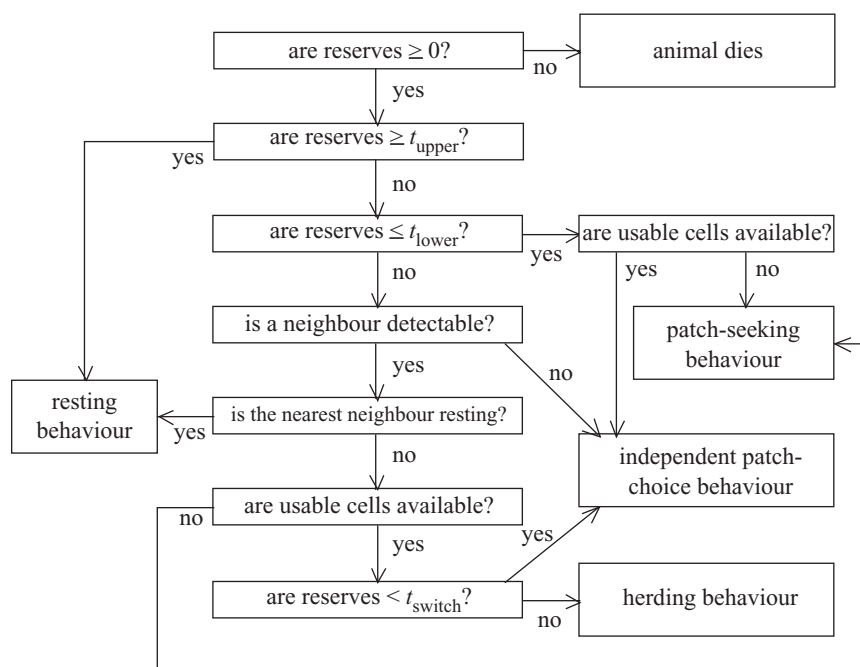


Figure 1. Summary of how an individual chooses its behaviour during a time-step of the model.

In this paper, we describe a spatially explicit model where foraging animals follow a rule-of-thumb behaviour that reflects the emphasis that an individual puts on protective herding versus individual foraging behaviour, with the individual basing its decisions upon both its energy reserves and the location and actions of its neighbours. We consider how this rule-of-thumb affects both the behaviour and foraging success of both individuals within groups and the groups themselves, in response to changes in the foraging–predation trade-off, the distribution of foraging resources in the environment, and the perceptual range over which individuals are able to detect colleagues and resources.

2. METHODS

(a) *Details of the model*

An individual-based model was created using NETLOGO, v. 1.3 for Mac OS X (Wilensky 1999). Here, we present a summary (full details are given in Appendix A). A number of simulations were conducted, as described below. At the beginning of a simulation, an environment was created consisting of a two-dimensional grid of square cells based on a torus. Within this environment, a set number of cells (SEED) were randomly selected, and the cells within a randomly chosen distance of each of these seeds were allocated a randomly chosen amount of energy (meaning that the number of cells containing energy increased with the value of SEED). Twenty individuals were then placed randomly in the environment, and their behaviours over 1500 consecutive time periods were modelled.

An individual based its behaviour primarily upon its energetic reserves, as summarized in figure 1. Rules are based upon those suggested by Rands *et al.* (2003), where individuals could choose between resting and foraging (both of which incurred an energetic cost, with foraging incurring the greater cost). At a given period of time (assuming that the animal made consecutive decisions about which action it should conduct until it made its next decision), if the individual's reserves were below a lower threshold t_{lower} ,

it foraged for food, by either staying in its current cell or moving to an unoccupied neighbouring cell if the contents of that cell were higher, and then harvested energy from its chosen cell. If the individual's reserves were above an upper threshold t_{upper} , it chose to rest for the period. If reserves were between these two thresholds, if there was no neighbour within a detection radius (DET) of the individual, the focal individual rested. If, however, a neighbour was visible, the focal individual copied the action of this neighbour: if the neighbour rested, so did the focal individual; whereas if the neighbour was foraging, the focal individual foraged. However, the form of foraging taken by the focal individual was dependent upon its energetic reserves. If reserves were below an intermediate threshold t_{switch} (where $t_{\text{lower}} \leq t_{\text{switch}} \leq t_{\text{upper}}$ and $t_{\text{lower}} < t_{\text{upper}}$), the individual foraged as described above, maximizing its energetic intake; if reserves were above t_{switch} , the forager instead conducted a selfish-herding behaviour and moved one cell towards a safer position (defined as the point between its two closest neighbours if two are detectable, or towards a single neighbour), harvesting energy from the cell it moved to. The exact value of t_{switch} was set using an independence parameter IND, defining the proportional value between t_{lower} and t_{upper} at which t_{switch} should occur (see Appendix A for details): with $\text{IND} = 0$, all individuals with reserves above t_{lower} conduct herding behaviour, while $\text{IND} = 1$ means all individuals between t_{lower} and t_{upper} conduct independent foraging. The value of t_{switch} could be used to explore differences in the perception of predation risk by foragers; e.g. when animals are in high-risk habitats or belong to a vulnerable age-sex class (low IND), or when animals are in low-risk habitats or belong to an age-sex class that is rarely predated (high IND). We assume that herding behaviour occurs when the animal has higher energy reserves, and therefore does not need to forage to avoid starvation.

An experimental dataset was generated using a crossed design. The detection radius of each forager, DET, was either 5 or 10 cells. The independence parameter, IND, took a value in the set $\{0.0, 0.25, 0.5, 0.75, 1.0\}$. The number of initial cell seeds in the environment, SEED, was a value from the set $\{25, 50, 75, 100\}$.

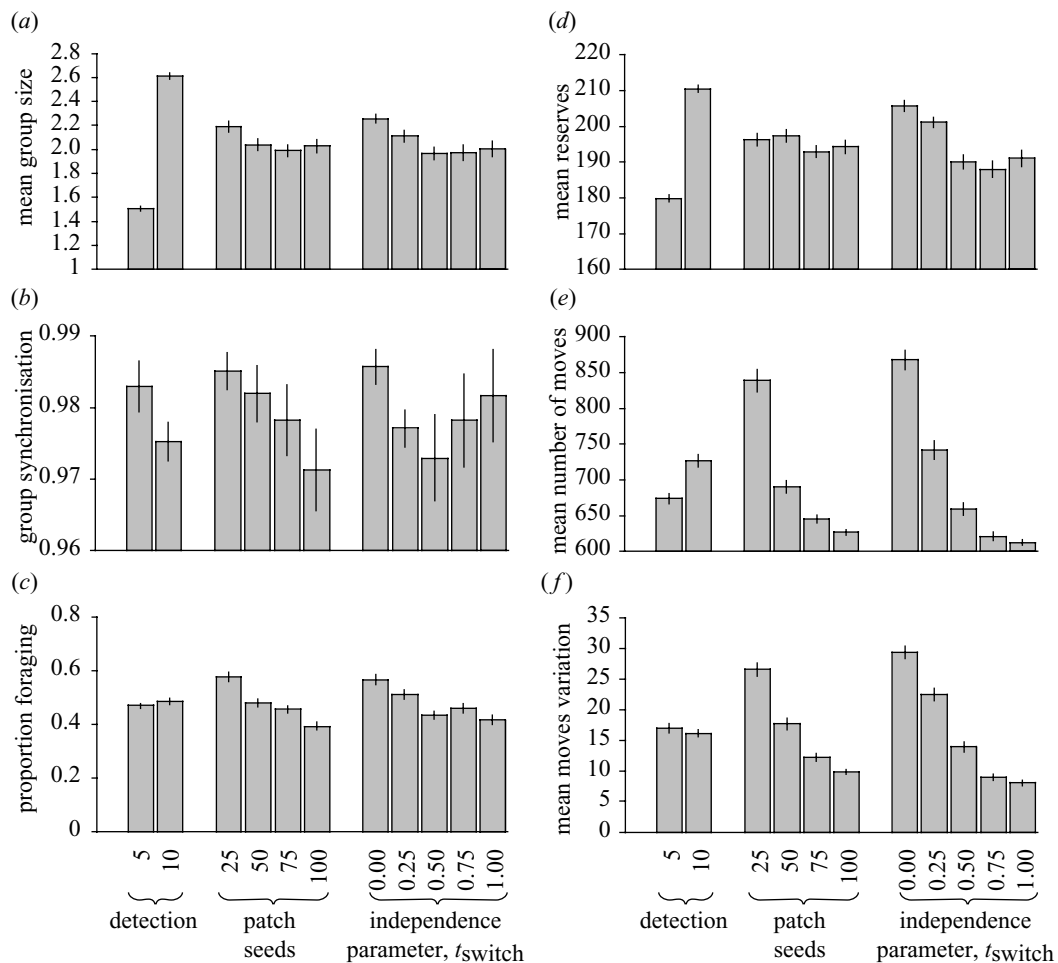


Figure 2. Effects of detection distance, number of initial cell seeds and the switch-point, t_{switch} , upon mean values (\pm s.d.) of: (a) nearest-neighbour cluster size; (b) degree of synchronization, ψ , within a multi-player nearest-neighbour cluster; (c) proportion of a simulation set foraging during period 1500; (d) energetic reserves of individuals; (e) number of moves made by an individual; and (f) variation in move numbers shown within a simulation set.

(This meant that the following proportions of the arena (\pm s.d.) contained energy when SEED = 25: 0.208 ± 0.036 ; 50: 0.358 ± 0.045 ; 75: 0.499 ± 0.046 ; 100: 0.614 ± 0.041 . The mean numbers of discrete patches when SEED = 25: 14.55 ± 2.14 ; 50: 17.00 ± 3.26 ; 75: 12.80 ± 4.76 ; 100: 6.95 ± 3.56 .) Twenty randomly generated environments (including the initial positioning of the 20 individuals within the simulation), denoted ENV, were simulated for each value of SEED. The parameter set chosen for the models presented was chosen arbitrarily: qualitatively similar results to those presented were obtained for a number of other simulations conducted with different initial parameter sets.

Statistics were determined based upon the positions and attributes of all survivors at period 1500 of each simulation. For each simulation, we determined: the mean cluster size (measured here as the number of individuals in a nearest-neighbour cluster, as described by Hamilton (1971), where a self-contained cluster is composed of all individuals that have at least one of the other members of the cluster as their nearest detectable neighbour); the mean energetic reserves of all the individuals within a simulation set; the mean number of moves made during the simulation by an individual and its variation within a simulation set (measured as the standard error of the mean); and the proportion of individuals foraging during the period. We also calculated the mean value for each simulation of a summary statistic, ψ , describing the degree of

synchronization within a detection nearest-neighbour cluster of at least two individuals, where $\psi = 2 \times [\max(\text{proportion foraging within cluster, proportion resting within cluster}) - 0.5]$. $\psi = 0$ shows complete asynchrony with half a cluster engaged in each activity, while $\psi = 1$ shows complete synchrony, regardless of the activity that all the members of the group are conducting.

(b) Statistical analysis

The data were analysed using MINITAB, V. 12.1 (Minitab Inc. 1998). General linear models were constructed, using the model DET|IND|SEED|ENV(SEED)-DET \times IND \times ENV(SEED), where ENV was a random factor. Where necessary, data were transformed to conform to model assumptions: the proportions foraging were arcsine transformed, mean reserves were exponentiated, the standard errors of the mean number of moves were log-transformed, and the mean numbers of moves were calculated to the power of -3.5 . Mean cluster sizes did not need adjusting. The mean value of ψ could not be adjusted suitably, and so a summary value of this term was calculated by averaging over the 20 ENV datapoints and fitted with the general linear model DET|IND|SEED-DET \times IND \times SEED. In discussing the results, significant interaction terms are discussed only where the effects seen gave further insights into the patterns observed.

Table 1. Results of general linear models for group size (the mean cluster size within a simulation, where e , the estimated error degrees of freedom of ENV(SEED), is 52.65); proportion foraging ($e = 78.67$); mean reserves ($e = 93.12$); mean number of moves ($e = 124.03$); and mean moves variation ($e = 117.94$). See text for details of transformations used.

	d.f.	group size		proportion foraging		mean reserves		mean number of moves		mean moves variation	
		F	p	F	p	F	p	F	p	F	p
DET	1,76	1693.83	<0.001	0.67	0.417	682.90	<0.001	541.83	<0.001	8.50	0.005
SEED	3,76	8.72	<0.001	20.67	<0.001	1.46	0.232	123.18	<0.001	128.05	<0.001
IND	4,304	18.11	<0.001	17.64	<0.001	33.76	<0.001	1131.83	<0.001	429.96	<0.001
ENV(SEED)	76, e	1.32	0.146	1.22	0.188	1.48	0.036	4.82	<0.001	1.53	0.018
DET \times SEED	3,76	4.82	0.004	2.25	0.089	7.89	<0.001	12.74	<0.001	29.20	<0.001
DET \times IND	4,304	30.79	<0.001	2.14	0.075	31.41	<0.001	17.69	<0.001	8.48	<0.001
DET \times ENV(SEED)	76,304	1.08	0.331	1.44	0.017	1.60	0.003	1.69	0.001	1.78	<0.001
SEED \times IND	12,304	1.59	0.093	5.62	<0.001	10.07	<0.001	23.19	<0.001	12.01	<0.001
IND \times ENV(SEED)	304,304	1.00	0.517	1.23	0.034	1.41	<0.001	1.85	<0.001	1.78	<0.001
DET \times SEED \times IND	12,304	1.22	0.266	1.23	0.256	1.02	0.434	1.82	0.044	0.99	0.454

Table 2. Results of general linear models, for the summarized proportion of individuals surviving and the summarized mean proportion of individuals synchronized in their behaviour within a multi-individual nearest-neighbour clusters, as summarized by the ψ statistic.

	d.f.	proportion synchronized	
		F	p
DET	1,12	2.38	0.149
SEED	3,12	1.41	0.287
IND	4,12	0.74	0.583
DET \times SEED	3,12	1.13	0.375
DET \times IND	4,12	0.78	0.558
SEED \times IND	12,12	0.36	0.956

4. RESULTS

Mean size of nearest-neighbour clusters was extremely dependent upon detection distance (figure 2*a*; table 1), where longer detection distances increased the likelihood that two animals would be within a suitable range for formation of nearest-neighbour clusters. Number of seeds had a significant effect upon cluster size, where the largest clusters were found in the environments with the lowest seed number (figure 2*a*); foragers tend to stay within a region of connected usable cells until all the resources within the region are depleted below a critical threshold; a lower initial seed count means that it is likely that within a region of usable connected cells there are fewer cells, and so foragers aggregated within these regions are more likely to be within detection range, leading to a higher number of animals sharing nearest neighbours. The value at which independent foraging switched to herding also had a significant effect (figure 2*a*; table 1), and larger clusters occurred when the switch-point was low (meaning that individuals would be more likely to keep within detection range of each other).

Synchrony levels within nearest-neighbour clusters with two or more members were very close to unity (figure 2*b*), meaning that all the members of a cluster were likely to be conducting the same behaviour. As would be expected, neither detection distance, initial number of seeds, nor the herding switch-point had a significant effect upon synchronization (table 2).

The proportion of a simulation set foraging was not significantly related to detection distance (figure 2*c*; table 1). The foraging proportion was highly related to the initial seeding of the environment (figure 2*c*; table 1), where the proportion foraging decreased with an increase in available cells (with more usable environment, individuals should spend less time in empty cells, and so should replenish energy reserves more rapidly, ultimately spending less time foraging). Similarly, the proportion foraging was greater where the independent foraging switch-point was low (figure 2*c*). In this case, individuals would be affected by both a reduction in intake caused by the shift from intake maximization to herding behaviour, and an increased likelihood of copying foraging behaviour (because a herding animal is more likely to be within detection range of a neighbour, meaning that it will copy the neighbour's behaviour if its own reserves are above t_{lower} rather than just rest, as would occur if there were no neighbour available to copy).

The mean energetic reserves of an individual within a simulation group were significantly lower when detection distance was low (figure 2*d*; table 1), which may be related to foragers travelling through regions of empty cells being less likely to detect and move to the cells with the highest energy content. Mean reserves were not significantly affected by the number of seeds in the environment (figure 2*d*). The switch-point between independent and herding behaviour had significant effects upon reserves and variation in reserves (figure 2*d*), where individuals with higher values of t_{switch} (and therefore more likely to be following independent foraging behaviour) had lower mean reserves, with reserves varying less within an environment.

The mean number of movements made by an individual increased with detection distance (figure 2*e*; table 1), and the variation within a simulation fell (figure 2*f*; table 1), presumably because the actions of individuals were more likely to be dictated by the actions of neighbours. Both mean number and variation in the number of moves fell with an increase in the initial number of seeds (figure 2*e-f*; table 1), where individuals were less likely to travel long distances over bad environments to find energy supplies. Mean number and variation in number of moves also fell with an increase in the switch-point between independent foraging and herding (figure 2*e-f*; table 1), with individuals becoming more likely to move to high-energy regions and remain within them until they were depleted, rather than being forced to move to low-energy regions closer to neighbours, and so work harder to maintain reserves at a suitable level.

5. DISCUSSION

This model has demonstrated that we can use state-dependent social foraging rules taken from optimality models to explore their effects upon group behaviour. Some of the results we present are intuitively obvious (such as many of the patterns seen in response to increasing the amount of energy available in the environment), but these results confirm that our model is following realistic patterns, and thus give us confidence that those model results that are less intuitively obvious are likely to be robust. Moreover, the model does present a number of predictions (discussed below) that are novel, relating to effects upon group size, and how individuals should behave, given differing levels of environmental predation risk.

In our model, group size is quantified using the surrogate measure of nearest-neighbour cluster size: the number of individuals connected by a nearest-neighbour network, as considered by Hamilton (1971). Although the size of clusters may appear small, it is a useful means of quantifying the size of the social groups formed. Social behaviour within the model framework depends upon the actions of nearest neighbours, and therefore it is more meaningful to consider a group as consisting of the set of individuals that can affect each other's actions, rather than using some arbitrary definition such as an aggregation of individuals within a specific radius of each other. The statistic allows us to quantify the degree of association seen between individuals, showing us that group size should increase with an increase in perceptual range, and should tend to fall with an increase in energy available in the environment, or an

increase in the degree of independent patch choice behaviour shown by an individual. Therefore, modulation of group size is an emergent feature of the simple rules followed by individuals (Camazine *et al.* 2001; Couzin & Krause 2003).

Theoretical investigations of stable group sizes have suggested that the optimal size (at which some fitness-related currency is maximized) is unlikely to be seen (Sibly 1983; Clark & Mangel 1984; Pulliam & Caraco 1984; Giraldeau & Gillis 1985; Kramer 1985; Giraldeau & Caraco 2000; Hamilton 2000). The model presented here does not make predictions about stable size because it is not an optimality model: it depends upon a mechanistic, rule-based procedure, rather than considering how the actions of the foragers could maximize some measure of their fitness (McNamara & Houston 1986). To interpret how the proximate mechanisms for group formation (modelled as the behaviours used within spatially explicit individual-based models) could have evolved, we must therefore consider how the responses of the foragers to external and internal stimuli are related to their fitness. This is indirectly addressed in the model described here, where the mechanisms leading to group formation are based upon a number of state-based rules that have been predicted by theory, where it is assumed that the animal is maximizing some measure of its fitness (Hamilton 1971; Houston & McNamara 1999; Rands *et al.* 2003). It would be desirable to base these rules upon the results of a single fitness-optimizing model that incorporated all the elements considered, rather than piecing together a rule based upon several models, but this is computationally complex, and arguably it is equally desirable to gain a thorough understanding of the effects of each of these separate elements before attempting to address them together within a single framework.

The model demonstrates that all the individuals of a given nearest-neighbour group will usually be conducting the same activity. This is perhaps predictable from the rule-of-thumb used, but it does demonstrate that synchronization within groups can occur. Synchronization of foraging behaviour is a phenomenon seen in many species (e.g. Rook & Huckle 1995; Ruckstuhl & Neuhaus 2002; Rands *et al.* 2004), but little work has been done on the synchronization of activity within local clusters of individuals; what our model suggests is that activities of nearest-neighbour groups may be highly synchronized, even if the behaviour of a local population is not.

Although the model described here did not include explicitly modelled predation events, we were nonetheless able to consider the indirect effects of differing environmental predation risks upon an individual's behaviour, such as the effects seen upon the number of movements made by individuals, and the likelihood that an individual foraged. The rule-of-thumb we used did not allow an individual to alter its behaviour in response to a predation event (and hence including explicit predation in the model would not have been enlightening, especially if predation events were rare), but it did reflect a range of feasible behavioural responses to differing risks of predation (reflected by the changing value of the independence threshold, at which a forager switched from independent foraging to selfish herding behaviour). Furthermore, differences in predation risk could also be reflected in an altered value of

t_{lower} (as demonstrated by Rands *et al.* 2004), which could also affect the group behaviours seen. The action an animal takes in the model we present is based primarily upon its energy reserves. Our model suggests that the reserve levels of a forager are inversely related to the threshold at which it should swap between maximizing its intake rate and seeking safety by approaching group members. If we interpret this to mean that the forager will have higher reserves when predation risk is high, this is contrary to predictions from theory (Houston & McNamara 1993, 1999; McNamara *et al.* 1994), where the optimal level of reserves falls as predation risk increases (although it should be noted that these models considered energetic expenditure as a mass-dependent cost; it is possible that including mass-dependence in the current model will have an effect upon results, although it is unclear whether mass-dependence would have a large qualitative effect within the dynamic game proposed by Rands *et al.* (2003)). Experiments testing these predictions by manipulating the perceived predation risk of individuals have shown that in some cases animals decrease their energetic reserves in response to an increase in risk. However, other experiments have yielded an increase in reserves (reviewed in Rands & Cuthill 2001). This has been suggested to be because the animals are responding to the predator interrupting their foraging routine, which can be countered by an increase in stored reserves (a result also predicted by theory). Although these experiments have not considered how social behaviour should affect reserves, the model presented here suggests that, with the added complexities of group-related behaviours, we should be careful how we apply the results of models optimizing the fitness of an individual acting alone to individuals interacting in groups.

In the model presented here, an individual bases its herding rule solely on its nearest neighbour or pair of neighbours. Other theoretical explorations of selfish herding behaviour have considered how simple movement rules can lead to realistic aggregations of animals (Morton *et al.* 1994; Viscido *et al.* 2001, 2002), and demonstrate that the greatest reductions in predation risk occur when an animal is able to base its movements relative to a larger number of close neighbours (although it should be noted that the assumptions made in these models have recently been criticised as being biologically unrealistic (see James *et al.* 2004)). In the model we present here, paying attention to one or two nearest neighbours proved sufficient to affect group sizes seen, but further realism in the rules used could be added in future models by allowing an individual to consider the locations and actions of other group members within detection range.

Through considering detection distance, the model showed that the perceptual range of the forager could be important in determining both the behaviour and decisions of an individual, and the size of the group. Perceptual ranges may be very important in determining the movement behaviours shown by an animal (Zollner & Lima 1999; Zollner 2000), especially where resources are clumped in a patchy environment. Perceptual ranges will also have effects upon group structure: if detection range is small but group benefits are high, groups will have to remain closely packed to allow cohesion, with repercussions on competition and visibility to predators. The limits of perceptual ranges, and therefore group structure, could

also be exacerbated by a spatially complex environment (such as thick vegetation). These findings also highlight the potential importance of contact calls and food calls in extending the perceptual range of social foragers, thus influencing group structure. For example, recent research has shown that such calls are given more frequently when group dispersion is high and when visibility conditions are poor (Uster & Zuberbühler 2001).

As urged by Krause & Ruxton (2002), it is important that individual-based models examining social behaviour attempt to use realistic rules. This allows us to make accurate predictions about group sizes and behaviours, which could be crucial for our understanding and management of natural populations (Conroy *et al.* 1995; Ruckelshaus *et al.* 1997). Models based upon rules derived from state-dependent optimality theory, such as the one presented here, are an effective way of incorporating this necessary element of realism.

This work was supported by a Natural Environment Research Council research grant awarded to G.C., R.A.P., J.M.R. and Rufus Johnstone (University of Cambridge). S.A.R. created the model in discussion with G.C. S.A.R. coded the simulations, conducted the statistical analysis, and was responsible for the initial draft of the manuscript. Many thanks to Sasha Dall, Andy Fenton, Rufus Johnstone, Jens Krause, and two anonymous referees for comments.

APPENDIX A. FURTHER DETAILS OF THE MODEL

A series of separate simulations were conducted, as described above. At the beginning of each simulation, a 51×51 -cell arena was created, with sides joined to form a torus. The arena was seeded by randomly choosing a set number (denoted SEED) of cells. Having chosen these, all the cells within a randomly chosen radius (using an integer-discretized normal distribution with a mean of 2.5 ± 1.2 cell length units (\pm s.d.)) of each seeded cell were filled with a randomly allocated integer amount of energy (using a discretized normal distribution with a mean of 10 ± 1.2 energy units). Twenty individuals were randomly placed at unoccupied points. Each of these individuals was randomly allocated an initial level of energy reserves (using a discretized normal distribution with a mean of 225 ± 37.5 energy units) and a randomly chosen initial direction of movement (in one of the four directions described below). Once initialized, a simulation was run for 1500 time-steps, where every individual conducted one behavioural action at each time-step.

At any given time-step, the action of an individual (to either rest or forage) was determined by its energy reserves, as summarized in figure 1. If reserves were above an upper satiation threshold t_{upper} of 300 units, the individual rested. If reserves fell to zero units, the individual was assumed to have starved to death, and was removed from the current simulation. For other reserve levels, the animal could choose to either rest or forage, according to the rules described below. If the individual rested, it did not move, and its energy reserves were reduced by $c_{\text{rest}} = 0.7$ units. If it foraged, reserves were reduced by c_{rest} plus an extra cost of foraging, $c_{\text{forage}} = 0.3$ units.

If the reserves of an animal fell at or below a lower threshold t_{lower} (set at 150 units), the animal foraged, regardless of the actions of any neighbours, using the behaviour

described below for selecting the best available cell. Above this threshold, the actions of an individual depended upon whether there was another animal within detection radius (defined as the area within a circle with a radius of DET, centred on the focal individual): if there were detectable neighbours, the focal individual copied the action (rest or forage) of the closest (if there was more than one nearest neighbour, the focal individual randomly chose which of these to copy); whereas if there was no detectable neighbour, the focal individual rested.

If an animal was foraging as a result of its copying the actions of a neighbour, its movement pattern while foraging was determined according to either the location of the best available food patch or the position of its neighbours (essentially, a trade-off between foraging and predation risk). The choice between these independent best-patch behaviour and risk-minimizing herding behaviours was governed by a switching threshold t_{switch} , determined using the independence parameter IND:

$$t_{\text{switch}} = \text{IND} (t_{\text{upper}} - t_{\text{lower}}) + t_{\text{lower}}.$$

If reserves fell below t_{switch} the forager conducted independent foraging; otherwise, it conducted herding behaviour.

If the forager chose to move to the best available cell, the energy contents of its current cell and those of the four neighbouring cells that were unoccupied were compared to ascertain which had the highest energy content: if its current cell had the highest value the forager remained in the cell; otherwise, it moved to the best neighbour, or randomly selected between best neighbours if there was more than one. If instead the forager chose to reduce its predation risk by herding, it moved to the usable neighbouring cell (where a usable cell is defined as one that contains at least a threshold minimum level of energy, set at two units) that took it closest to the point midway between the two nearest neighbours within detection range (or towards its neighbour if only one was detectable).

If at all possible, a forager should move to an unoccupied usable cell: this behaviour was also followed when herding, even if this forced the forager to move in the direction away from its colleagues (this behaviour was necessary to avoid excessive numbers of individuals starving during the simulation). If the individual could not move to a usable cell (because either no neighbouring cells contained sufficient energy, or all of those containing sufficient energy were already occupied by a colleague), it moved to the neighbouring unoccupied cell (or randomly chose between them if several were available) that took it closest to the cell within its radius of detection that had the highest amount of energy. If no suitable cells were detectable, the animal moved according to a sinuous random walk, with a 50% chance of moving one cell forwards in the same direction it had moved in the previous round, and 25% chances each of moving one cell forwards at 90° or 270° to this previous direction.

Once a forager had moved (or decided to stay in its current cell), it harvested two units of energy from the target patch (and the cell's energy content was reduced by the same amount), which were added to its current energy reserves. Once all the live foragers within the simulation had conducted their movement for the time-step, any cells within the arena that had energy levels below their initially

determined level at the start of the simulation had their energy levels increased by the minimum value of either 0.05 units or the amount needed to achieve the initial level.

REFERENCES

- Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2001 *Self-organization in biological systems*. Princeton University Press.
- Clark, C. W. & Mangel, M. 1984 Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**, 626–641.
- Clark, C. W. & Mangel, M. 2000 *Dynamic state variable models in ecology: methods and applications*. New York: Oxford University Press.
- Conroy, M. J., Cohen, Y., James, F. C., Matsinos, Y. G. & Maurer, B. A. 1995 Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecol. Appl.* **5**, 17–19.
- Couzin, I. D. & Krause, J. 2003 Self-organization and collective behavior in vertebrates. *Adv. Stud. Behav.* **32**, 1–75.
- Cowlshaw, G. 1997 Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**, 667–686. (doi:10.1006/anbe.1996.0298)
- Ekman, J. & Rosander, B. 1987 Starvation risk and flock size of the social forager: when there is a flocking cost. *Theor. Popul. Biol.* **31**, 167–177.
- Flierl, G., Grünbaum, D., Levin, S. & Olson, D. 1999 From individuals to aggregations: the interplay between behavior and physics. *J. Theor. Biol.* **196**, 397–454. (doi:10.1006/jtbi.1998.0842)
- Giraldeau, L.-A. & Caraco, T. 2000 *Social foraging theory*. Princeton University Press.
- Giraldeau, L.-A. & Gillis, D. 1985 Optimal group size can be subtle: a reply to Sibly. *Anim. Behav.* **33**, 666–667.
- Hamilton, I. M. 2000 Recruiters and joiners: using optimal skew theory to predict group size and the division of resources within groups of social foragers. *Am. Nat.* **155**, 684–695.
- Hamilton, W. D. 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311.
- Higashi, M. & Yamamura, N. 1993 What determines group size? Insider–outsider conflict and its resolution. *Am. Nat.* **142**, 553–563.
- Houston, A. I. & McNamara, J. M. 1993 A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scand.* **24**, 205–219.
- Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.
- James, R., Bennett, P. G. & Krause, J. 2004 Geometry for mutualistic and selfish herds: the limited domain of danger. *J. Theor. Biol.* **228**, 107–113. (doi:10.1016/j.jtbi.2003.12.005)
- Juanico, D. E., Monterola, C. & Saloma, C. 2003 Allelomimicry as a generic clustering mechanism for interaction agents. *Physica A* **320**, 590–600. (doi:10.1016/S0378-4371(02)01556-X)
- Kramer, D. L. 1985 Are colonies supraoptimal groups? *Anim. Behav.* **33**, 1031–1032.
- Krause, J. 1994 Differential fitness returns in relation to spatial position in groups. *Biol. Rev.* **69**, 187–206.
- Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford University Press.
- McNamara, J. M. & Houston, A. I. 1986 The common currency for behavioral decisions. *Am. Nat.* **127**, 358–378.
- McNamara, J. M., Houston, A. I. & Lima, S. L. 1994 Foraging routines of small birds in winter: a theoretical investigation. *J. Avian Biol.* **25**, 287–302.
- Minitab Inc. 1998 *MINITAB 12.1 for Windows 95/NT*. Philadelphia, PA: State College.

- Morton, T. L., Haefner, J. W., Nugala, V., Decimo, R. D. & Mendes, L. 1994 The selfish herd revisited: do simple movement rules reduce relative predation risk? *J. Theor. Biol.* **167**, 73–79. (doi:10.1006/jtbi.1994.1051)
- Pulliam, H. R. & Caraco, T. 1984 Living in groups: is there an optimal group size? In *Behavioural ecology: an evolutionary approach*, 2nd edn (ed. J. R. Krebs & N. B. Davies), pp. 122–147. Oxford: Blackwell Science.
- Rands, S. A. & Cuthill, I. C. 2001 Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. *Proc. R. Soc. Lond. B* **268**, 1783–1790. (doi:10.1098/rspb.2001.1653)
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. 2003 The spontaneous emergence of leaders and followers in a foraging pair. *Nature* **423**, 432–434. (doi:10.1038/nature01630)
- Rands, S. A., Cowlshaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. 2004 Leadership and synchronisation in animals that are not equal. (In preparation.)
- Rook, A. J. & Huckle, C. A. 1995 Synchronization of ingestive behaviour by grazing dairy cows. *Anim. Sci.* **60**, 25–30.
- Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997 Assessing the data requirements of spatially explicit dispersal models. *Conserv. Biol.* **11**, 1298–1306.
- Ruckstuhl, K. E. & Neuhaus, P. 2002 Sexual segregation in ungulates: a comparative test of three hypotheses. *Biol. Rev.* **77**, 77–96. (doi:10.1017/S1464793101005814)
- Sibly, R. M. 1983 Optimal group size is unstable. *Anim. Behav.* **31**, 946–951.
- Stankowich, T. 2003 Marginal predation methodologies and the importance of predator preferences. *Anim. Behav.* **66**, 589–599. (doi:10.1006/anbe.2003.2232)
- Uster, D. & Zuberbühler, K. 2001 The functional significance of Diana monkey 'clear' calls. *Behaviour* **138**, 741–756.
- Viscido, S. V., Miller, M. & Wetthey, D. S. 2001 The response of a selfish herd to an attack from outside the group perimeter. *J. Theor. Biol.* **208**, 315–328. (doi:10.1006/jtbi.2000.2221)
- Viscido, S. V., Miller, M. & Wetthey, D. S. 2002 The dilemma of the selfish herd: the search for a realistic movement rule. *J. Theor. Biol.* **217**, 183–194. (doi:10.1006/jtbi.2003.3025)
- Wilensky, U. 1999 *NETLOGO*. Evanston, IL: Center for Connected Learning and Computer-based Modeling, Northwestern University. See <http://ccl.northwestern.edu/netlogo/>.
- Zollner, P. A. 2000 Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecol.* **15**, 523–533.
- Zollner, P. A. & Lima, S. L. 1999 Search strategies for landscape-level interpatch movements. *Ecology* **80**, 1019–1030.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.